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Entogoniopsis gen. nov. and *Trilamina gen. nov.* (Bacillariophyta): a survey of multipolar pseudocellate diatoms with internal costae, including comments on the genus *Sheshukovia* Gleser

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Abstract

We present the results of an extensive light-(LM) and scanning electron microscope (SEM) study of internally costate pseudocellate multipolar diatoms previously placed within *Biddulphia*, *Entogonia*, *Sheshukovia* and *Triceratium*. For the first time, we critically examine the poorly known genus *Sheshukovia*. We find that the separation of *Sheshukovia* from *Triceratium* is justified, as advocated by Gleser (1975, 1984), but also show that *Sheshukovia* as circumscribed by Gleser (1975, 1984) is a heterogenous taxon comprising at least three morphologically distinct groups. In order to clarify the confused taxonomy of pseudocellate multipolar diatoms, a preliminary phylogenetic analysis is presented, including *Triceratium*, *Sheshukovia*, *Entogonia*, *Medlinia* and two new closely related genera proposed here: *Entogoniopsis* and *Trilamina*. Both new genera have valvocopulae that attach to costae on the valve interior by means of a variety of clasping devices. *Entogoniopsis*is is characterized by areolate valves and a twofold mechanism for valvocopula attachment, whereas *Trilamina* possesses extensive hyaline areas and a threefold valvocopula attachment mechanism. The twofold mechanism for valvocopula attachment in *Entogoniopsis*, and the threefold valvocopula attachment mechanism in *Trilamina* are here considered synapomorphies supporting the monophyly of the respective taxon. The morphology of 19 species, four of which are new, is documented using both LM and SEM and a further 18 taxa are transferred from elsewhere, observations being based on literature survey and/or LM examination. When original material is available, taxa are typified. Two new morphological terms are proposed: a *trifolium* is a triradiate raised sector located in the central part of undulate valve faces in some species of *Entogoniopsis*; a *fossa* is a circumferential invagination of the advalvar edge of the valcocopula. These features are found in both new genera proposed herein.

Key words: multipolar centric diatoms, pseudocelli, internal costae, *Triceratium, Entogoniopsis*, *Trilamina*, *Sheshukovia*, taxonomy, morphology, phylogenetic analysis

Introduction

For several decades in the early history of diatom investigations, most species of multipolar centric diatoms were placed in the genus *Triceratium* Ehrenberg (1839: 156; Figs 1–2), for instance: *Triceratium arcticum* Brightwell (1853: 250, pl. I, fig. 11a–b), *T. blanditum* Greville (1861a: 45; 1861b: 72, pl. VIII, fig. 17), or *T. sexapartitum* Grove & Sturt (1887c: 145, pl. XIV, fig. 64). As a consequence, there are now several hundred names with little understanding of how many are valid, and no sufficient understanding of what generic sub-divisions there may be amongst those species (see the online Catalogue of Diatom Names; Fourtanier & Kociolek 2009, 2011). Without a doubt, *Triceratium* is in need of revision. Early attempts at this were based either on transferring groups of *Triceratium* spp. to other genera, such as *Biddulphia* S.F. Gray (1821: 294; see Boyer 1900) or *Entogonia* Greville (1863: 235; Figs 3–5), or the creation of new genera, such as *Trigonium* Cleve (1867: 663), *Amphitetras* Ehrenberg (1840: 42), sometimes treated as subgenera (see De Toni 1894). Even in the 1970s, with the rapid development of diatom biostratigraphic schemes and palaeoceanographic proxies, the distinction between *Triceratium* and other multipolar genera (e.g., *Trinacria* Heiberg 1863: 49) was not consistently applied. During this period, Gleser (1975, 1986) made an attempt to revise *Triceratium sensu lato* and its systematic position. For one group of species, she proposed the new genus *Sheshukovia* Gleser (1975: 1307) based on the presence of polar pseudocelli and a poroid valve structure (Figs 6–7), as opposed to pseudoloculate valve structure of *Triceratium sensu stricto* (Figs 3–5). At first, the new genus included five taxa (Gleser 1975); subsequently, however, Gleser (1984) transferred a further 37 taxa, most of which are extinct.

Since its description, *Sheshukovia* has been subject to some discussion, much of it connected with nomenclatural issues (see e.g., Fenner 1994: 293). Gleser chose *Sheshukovia kolbei* var. *uralense* (Jousé) Gleser (1975: 1307; basionym: *Triceratium kolbei* var. *uralense* Jousé 1951: 34) as the generitype of *Sheshukovia*, even though because of insufficient data *T. kolbei* var. *uralense* was only provisionally included as part of *T. kolbei* Hustedt (ex Simonsen 1987: 127; invalidly published in Hustedt 1930: taf. 372, fig. 4). Later, Gleser (1984) indicated that, alternatively, *Sheshukovia kolbei* (Hustedt) Gleser (1984: 294; basionym: *Triceratium kolbei* Hustedt ex Simonsen 1987; Figs 6–7) should be the type of the genus. It is beyond the scope of this paper to settle the nomenclatural issues associated with the type of *Sheshukovia*. For the purpose of this study, we follow Gleser (1984) and treat *S. kolbei* as the type species.